Rootstock effect on growth of apple scions with different growth habits

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Abstract

Apple scions with diverse growth habits were grafted on various size-controlling rootstocks and morphological characteristics were measured after 6 years of growth in the field. Scion had more influence than rootstock on monthly growth rate. Across all rootstocks, scions with spreading growth habits grew rapidly in April and May and achieved most seasonal growth earlier than scions with upright growth habits that grew slowly early in the season. In all growth habits and rootstocks, growth rate slowed appreciably but did not cease by August and growth did not terminate earlier for any one scion–rootstock combination. Across all scions, the dwarfing rootstock, M.9, consistently had the lowest and seedling rootstock had the greatest tree height and trunk diameter. However, no one size-controlling rootstock consistently influenced dates of bud break and full bloom, shoot elongation rate, or duration of growth. Tree growth form was not fundamentally affected by rootstock. Significant interactions indicated that effects of size-controlling rootstock on components of shoot growth will vary with apple tree growth habit. These effects on phenology and development can be significant to growers and may assist breeders in developing new apple cultivars.
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1. Introduction

Rootstocks are used to propagate scions of preferred cultivars, improve fruit tree tolerance to environmental stress, and to control tree size (Webster, 2001). Size-controlling rootstocks are economically important for high density apple tree plantings that may produce larger fruit and more fruit per hectare (Autio et al., 2000; Webster and Wertheim, 2003). Improved fruiting from size-controlling rootstocks has been accompanied by altered tree morphology associated with modification of dry weight distribution, rate and duration of shoot elongation, and branch angle (Schechter et al., 1991; Strong and Miller-Azarenko, 1991; Warner, 1991; Webster and Wertheim, 2003).

Research on rootstock–scion interactions demonstrated that rootstock had more influence than scion on tree weight and growth rate in young apple trees but scion more strongly influenced duration of growth (Vyvyan, 1955). In a study of phenological effects, rootstock did not regulate dates of bud break, full bloom, and establishment of full canopy in 'Starkspur Supreme Delicious' (Schechter et al., 1991). Collectively, research has shown that growth control can be provided by a particular rootstock but the amount of control depends on the apple cultivar that is grafted on to the rootstock. Early in their use, Malling rootstocks were recognized to have different size-controlling effects on different apple varieties (Zeiger and Tukey, 1960). Rootstock–scion interactions also have been observed when dwarfing rootstock flattened branch orientation more in apple trees with upright growth habits (e.g. 'Sturdeespur Delicious') than spreading growth habits (e.g. 'Empire') (Warner, 1991). Rootstocks have been found to affect different components of scion shoot growth (e.g. number but not length of internodes of annual growth, Webster, 2001) but rootstock effects on shoot growth components in scions with different growth habits is not established. Since apple cultivars may have different canopy dimensions and shapes (i.e. growth habits), rootstock effects that may alter morphology or phenology of different growth habits would be relevant to breeders, researchers, and growers.

Branch orientation is a distinctive characteristic of apple tree canopies with different growth habits and branch orientation can influence growth. Shoot growth within a single tree ('Red Prince Delicious') had less growth if the branch natural orientation was more horizontal than vertical Myers and Ferree

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(1983). Many studies have demonstrated that branches forced to a horizontal orientation tend to grow less than branches with a more upright orientation (Miller and Tworkoski, 2003). Differences in shoot orientation, growth rate, and branching are at least partly regulated by apical dominance and apical control which strongly influence tree growth habit (Zimmermann and Brown, 1971). Many experiments have focused on effects of size-controlling rootstocks on growth and yield of commercial apple cultivars but interactive effects of rootstock and scion with different growth habits have not been elucidated.

In the current experiment, the goal was to improve understanding of rootstock effects on apple scions with different growth habits to assist with rootstock selection and to facilitate future study of the mechanisms of rootstock-regulated processes. The hypothesis was that dwarfing root-stock would decrease branch angles and inhibit stem elongation more in upright than in wide angled trees. The objectives were to: (1) compare growth rates and termination of growth of branches of different rootstock–scion combinations and (2) determine rootstock effects on components of seasonal growth of scions with different growth habits.

2. Materials and methods

The scions used in this experiment came from five trees with different growth habits that were planted at the Beltsville Agricultural Research Center, Beltsville, MD, in 1975 (Zagaja and Faust, 1983) (Table 1). The trees were seedlings from an F2 generation of hybrids produced by sibcross selections from a 'Goldspur Delicious' × 'Redspur Delicious' progeny (Faust

and Steffens, 1993). Bud wood was collected in 1996 and "T-budded" to rootstocks EMLA.7 (M.7) semi-dwarfing; EMLA.111 (MM.111) semi vigorous; M.9 very dwarfing (all 1-year rooted layers, 8–12 mm) and *Malus antanovka* (2 years transplanted, 6–10 mm) (Grootendorst Nurseries Inc., Lakeside, MI 49116). The resulting trees provided a range of growth habits from upright and narrow to spreading and wide canopies (Fig. 1). Ten of each scion–rootstock combination was planted in a nursery on 14 May 1996. The compound trees were fertilized and irrigated according to current nursery practices.

Trees were planted on 21 October 1997 into an orchard with 4.9 m × 4.9 m spacing. 'Golden Delicious' and 'Delicious' trees budded to EMLA.111, EMLA.7, and seedling rootstocks from a commercial nursery were included in the planting for comparison. The experimental layout was randomized with blocking based on location in the orchard. Trees were not pruned but were maintained in 2-m wide vegetation free strips using preemergence herbicides in spring and spot applications of paraquat (1,1′-dimethyl-4,4′-bipyridinium) or glyphosate (*N*-(phosphonomethyl)glycine), as needed. Insect and disease pressure was managed following WVU-recommended protocols (Pfeiffer, 1998). Tree survival varied with growth habit and was not affected by rootstock. Survival rates of transplanted trees on 13 October 2003 were 40, 90, 70, and 80% for upright-round (UR), upright-narrow (UN), spreading-round (SR), and spreading-weep (SW) growth habits, respectively, for all rootstocks.

Tree growth was measured in April 2003 and 2004. The growth variables included tree height, canopy width, trunk

Table 1
Characteristics of F2 generation of 'Goldspur' and 'Redspur' apple trees propagated by Zagaja and Faust (1983) and selected in 1996 as source for bud wood for scion–rootstock interaction experiment

Scion	Height (m)	Canopy width (m)	Shoot length (cm/1-year)	Internode (no./shoot)	Internode length (mm)	Branch angle (from horizontal)	Trunk diameter (cm)	Canopy description
Upright-round	3.3	2.3	21	36	5.8	61	10.6	Round, upright, thin branches
Upright-narrow	3.5	2	46	54	8.5	61	12.7	Columnar, thick branches
Spreading-round	2.7	2.9	18	30	6.0	17	7.8	Open, spreading
Spreading-weep	2.9	4.1	18	14	12.9	16	12.5	Open, weeping

Fig. 1. Upright-narrow (left) and spreading-round (right) growth habits grown on seedling rootstock in 2003.

diameter 10 cm above the graft union, crotch angle from the trunk of three main architectural branches per tree, growth of 10 shoots per tree from the previous season (2002 and 2003 length and number of internodes), and number of flower clusters per limb cross-sectional area of three limbs. Average internode length was calculated by dividing shoot length by the number of internodes per shoot. In the 10 shoots measured in April 2004 additional measurements included the number and length of branches or spurs and number and length of internodes from apex to first lateral branch. In October 2003 and 2004, total fruit number and weight per tree were measured. Fruit yield was expressed on a trunk cross-sectional area basis by dividing number or weight per tree by the trunk area using the measured trunk diameter. Treatment effects were evaluated by the general linear model procedure and means were separated using the Duncan's multiple range test (SAS, 2001).

During 2004, 10 branches per tree were labeled and growth was measured each month from April through October. Five branches from the top-most portion of the tree canopy and five from the mid canopy were selected; all were from the outer perimeter of the canopy. The monthly growth measurements were converted to percent of total 2004 growth per branch and a regression equation was calculated for each scion–rootstock combination based on the equation: $y = \ln(a + bx)$ (SigmaPlot 2000 ver. 6.00; SPSS Inc.). The coefficients (a and b) were used

to calculate the number of days (x) required to attain 50% of full season growth ($y = 0.50$). All equations had an r^2 of 0.97 or greater. The number of days to 50% of full season growth per tree for rootstock-growth habit combinations was statistically analyzed as previously described.

Beginning on 4 April 2005 (time zero; i.e. no buds had yet broken), the number of growing buds and open king flowers were counted on 20 buds per tree in 3 replications per scion–rootstock combination. Buds were from the north-facing side of the canopy and were located on lateral shoots that were no longer than 5 cm and on 1-year-old shoots. Measurements were taken on Monday, Wednesday, and Friday each week and the bud break and flowering were characterized by a sigmoid equation: $y = a/(1 + e^{-(x-x_0/b)})$ (SigmaPlot 2000). The sigmoid regression coefficients (a and b) were used to estimate the time (x) to 50% bud break and 50% flowering ($y = 0.50$) for each tree and scion–rootstock effects were tested with Proc GLM (SAS, 2001) and separated by the LS Means procedure.

3. Results

3.1. Annual growth and tree dimensions

Relative size-controlling effects of rootstocks on shoot growth were consistent within each growth habit from 2002
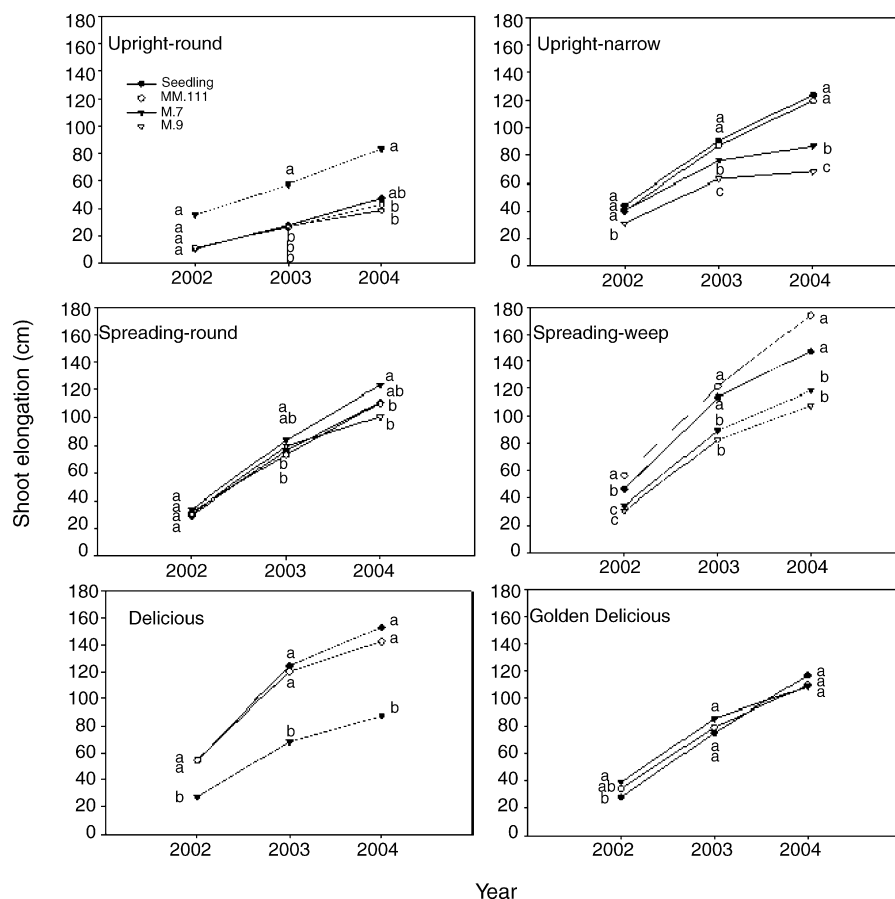

Fig. 2. Cumulative average growth of 1-year-old shoots of four growth habits on four rootstocks and two cultivars on three rootstocks. Within each year and growth habit, means followed by the same letter do not differ at the 95% level of significance.

through 2004 (Fig. 2). However, no single rootstock consistently had the most shoot growth for all growth habits. Greatest shoot growth included the following rootstock-growth habit combinations: M.7-UR, seedling-UN, MM.111-SW, and M.7-SR. Height, canopy diameter, and trunk diameter were similarly affected by rootstock within each growth habit but, as with annual shoot growth, no rootstock was uniformly the greatest size across growth habits (Table 2).

Trees grown on M.9 were generally the smallest but the amount of reduction differed between scions (Table 2). For example, M.9 reduced height of UR, UN, SW, and SR by an average of 34, 18, 36, and 13% compared with seedling rootstock. Tree heights were reduced similarly in UR and SW growth habits even though they differed dramatically in average branch length, diameter and internode length, and with branch angle (Tables 2 and 3). The amount of tree height reduction was not associated with growth habits that were more upright or spreading. In the current experiment, M.9 rootstock generally had the shortest tree but tallest trees were grown on seedling, MM.111, or M.7 rootstocks.

3.2. Seasonal growth patterns

3.2.1. Monthly growth

In April, scions with spreading growth habits ('Golden Delicious', SW, and SR) elongated more than four-times faster than scions with upright growth habits ('Delicious', UN, UR) (Fig. 3). Growth rates became more similar among the growth habits after May and rootstock effects were evident (Fig. 3). Growth rate was reduced by M.9 compared with M.7 in UN, UR, and SR but not in SW growth habits. Growth rates of M.7 were consistently less than MM.111 and seedling rootstocks in UN and SW but similar differences were not seen in UR and SR growth habits. For example, growth rates of M.7 exceeded MM.111 in SR and UR during July and August. Changes in growth rate over time differed with growth habit and rootstock.

Growth rate of UN increased from April through June with MM.111, M.7 and seedling rootstocks and decreased in July (Fig. 3). On M.9, UN growth rate decreased each month throughout the season. Growth rate of the spreading growth habits (SW, SR, and 'Golden Delicious') decreased by 40–93% between April and May and continued to decrease throughout

Table 2
Tree height, canopy diameter, and growth of 1-year-old shoots and yield on a trunk diameter cross-sectional area (tcsa) basis of four apple growth habits on four rootstock and two apple cultivars on three rootstocks

Rootstock	Scion					
	Upright-round	Upright-narrow	Spreading-round	Spreading-weep	'Delicious'	'Golden Delicious'
Height (m)						
M.9	1.1 c	2.7 c	3.8 b	3.7 d	No tree	No tree
M.7	2.0 a	3.0 b	3.4 c	4.2 c	3.9 c	4.2 a
MM.111	1.7 b	3.0 b	4.3 a	4.9 b	4.5 b	3.6 b
Seedling	1.8 ab	3.3 a	4.3 a	5.8 a	4.6 a	3.7 b
Canopy diameter (m)						
M.9	0.5 c	1.4 c	2.5 c	2.0 c	No tree	No tree
M.7	1.8 a	1.6 b	2.3 d	2.3 b	1.8 a	2.0 a
MM.111	1.4 c	1.6 b	2.8 b	2.0 c	1.6 b	1.9 b
Seedling	1.7 b	1.8 a	2.9 a	2.8 a	1.6 b	2.0 a
Trunk diameter (mm)						
M.9	48.5 c	73.3 c	85.9 c	67.6 d	No tree	No tree
M.7	54.0 b	88.7 b	91.6 b	82.9 c	85.4 c	94.4 a
MM.111	55.9 b	84.9 b	93.5 b	90.3 b	92.3 b	82.9 c
Seedling	59.3 a	102.4 a	106.9 a	125.4 a	100.3 a	89.2 b
Growth of 1-year-old shoot (cm/cm^2 tcsa)						
M.9	0.6 b	0.1 d	0.4 b	0.9 a	No tree	No tree
M.7	1.1 a	0.3 c	0.6 a	0.6 b	0.4 a	0.3 b
MM.111	0.7 b	0.7 a	0.7 a	1.0 a	0.3 a	0.6 a
Seedling	0.7 b	0.5 b	0.4 b	0.3 c	0.4 a	0.7 a
Yield (no./cm^2 tcsa)						
M.9	0 a	0.2 b	2.2 d	3.5 a	No tree	No tree
M.7	0 a	0 b	7.6 b	3.6 a	2.8 a	1.3 c
MM.111	0 a	0.8 a	9.4 a	3.4 a	2.3 b	2.9 b
Seedling	0 a	0 b	5.3 c	1.6 b	0.6 c	6.5 a
Yield (kg/cm^2 tcsa)						
M.9	0 a	0.03 b	0.22 c	0.47 a	No tree	No tree
M.7	0 a	0 b	0.69 a	0.43 a	0.42 a	0.16 c
MM.111	0 a	0.07 a	0.80 a	0.42 a	0.31 b	0.40 b
Seedling	0 a	0 b	0.42 b	0.20 b	0.09 c	0.85 a

The main effects of scion (S) and rootstock (R) and the S × R interaction were significant for all variables at $P > F = 0.001$. Within each growth habit (column) and variable, means followed by the same letter do not differ at the 95% level of confidence.

Table 3
Characteristics of 1-year-old shoots and branch angle of four apple growth habits on four rootstock and two apple cultivars on three rootstocks

Scion	Rootstock	Length (cm)	Nodes (no.)	Basal diameter (mm)	Average internode length (cm)	Branch angle (°)
Upright-round	M.9	16 b	55 a	5 a	0.3 b	42 a
	M.7	22 a	46 ab	5 a	0.5 a	39 a
	MM.111	15 b	41 b	4 ab	0.4 ab	32 a
	Seedling	18 ab	39 b	4 b	0.4 a	40 a
Upright-narrow	M.9	32 c	59 d	11 b	0.5 c	50 a
	M.7	36 b	62 c	12 a	0.6 b	50 a
	MM.111	47 a	65 b	13 a	0.7 a	52 a
	Seedling	47 a	67 a	12 a	0.7 a	42 a
Spreading-round	M.9	49 ab	31 b	7 ab	1.6 a	82 a
	M.7	50 a	37 a	7 a	1.4 b	84 a
	MM.111	41 b	30 b	6 b	1.4 b	79 a
	Seedling	47 b	34 a	6 b	1.4 b	88 a
Spreading-weep	M.9	52 b	40 c	9 ab	1.4 ab	71 a
	M.7	55 b	42 b	8 b	1.3 b	75 a
	MM.111	65 a	44 ab	9 a	1.5 a	74 a
	Seedling	68 a	46 a	9 a	1.5 a	72 a
'Delicious'	M.7	41 b	44 b	8 b	0.9 b	62 a
	MM.111	65 a	52 a	9 a	1.3 a	59 a
	Seedling	70 a	54 a	9 a	1.3 a	63 a
'Golden Delicious'	M.7	47 a	34 b	8 a	1.4 a	77 a
	MM.111	45 a	44 a	8 a	1.0 b	62 b
	Seedling	48 a	46 a	8 a	1.0 b	62 b
P > F						
Scion (S)		0.01	0.01	0.01	0.01	0.01
Rootstock (R)		0.01	0.01	0.51	0.27	0.19
S × R		0.01	0.01	0.01	0.01	0.29

Within each growth habit and variable (column), means followed by the same letter do not differ at the 95% level of confidence.

the season. As with UN, M.9 rootstock reduced growth rate of SW and SR compared with MM.111 in April through June. Unlike UN, where M.9 rootstock reduced growth rate throughout the season, rootstock caused little or no growth rate reduction from July through September in SW and SR growth habits.

Rootstock effects on the number of days needed for 50% of full seasonal shoot elongation varied with scion. There was little difference among rootstocks in UR (54–59 days) and 'Delicious' (50 days for all rootstocks) and comparatively larger rootstock differences for UN (50 days on M.9 to 66 days on M.7). The time needed to achieve 50% of seasonal shoot elongation was shorter in the spreading growth habits, reflecting the greater growth rates early in the season. Times to 50% total seasonal shoot elongation in the SW growth habit were 33, 44, 40, and 37 days for seedling, MM.111, M.7, and M.9 rootstocks, respectively. In the SR growth habit, the range of times to 50% of seasonal shoot elongation was 27–37 days (M.9 and M.7, respectively). Early season rapid growth may contribute to a spreading growth habit. Whole season shoot length and diameter were similar in 'Delicious' and SW but branch angles were wider in SW (Table 3). Rapid branch elongation may have preceded diameter growth in SW resulting in branches deflecting downwards.

3.2.2. Time to bud break

Significant scion, rootstock, and interaction effects were found for number of days to bud break and treatment effects are

reported as different only when the response differences due to chance alone do not exceed the 5% level of significance. Time to 50% bud break per tree was affected by rootstock in UN but not in SW and SR growth habits which averaged 2.6 days (7 April 2005). In UN, rate of bud break was slower than the spreading growth habits and was earlier on M.7 and M.9 (3.7 days) than on MM.111 and seedling rootstock (8.8 days). Time to bud break did not appear to be related to initial monthly growth rate. Bud break was early and growth was rapid in SW and SR but in UN, the earlier bud break on M.7 and M.9 was accompanied by a slower growth rate (Fig. 3). Upright-round trees could not be evaluated in 2005 due to insufficient number of trees. In 'Golden Delicious', bud break was earlier on MM.111 and M.7 rootstocks (2.5 days) than on seedling rootstock (6.9 days). In 'Delicious' bud break was earlier on M.7 (2.5 days) than on MM.111 (3.7 days) and bud break was intermediate on seedling rootstock (2.9 days). Rootstock type did not consistently affect bud break and scion seemed to have greater effect. For example, 50% bud break was later in UN than any other growth habit for any given rootstock.

3.2.3. Flowering

As with bud break, time to 50% flowering per tree was not consistently influenced by rootstock when the same statistical criteria were used. On M.7 rootstock, the time to 50% flower development was earlier in 'Golden Delicious' (17.6 days) and
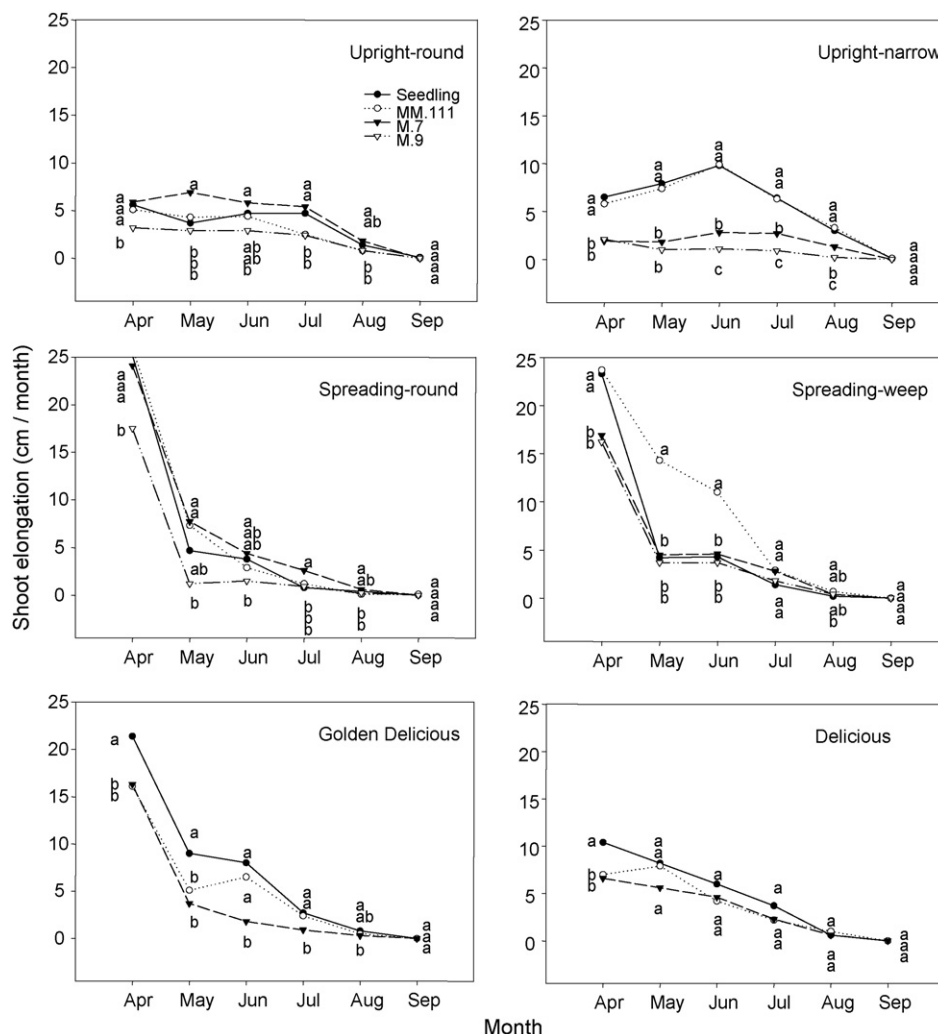
Fig. 3. Monthly shoot elongation rate of 1-year-old shoots of four growth habits on four rootstocks and two cultivars on three rootstocks. Within each month and growth habit, means followed by the same letter do not differ at the 95% level of significance.

'Delicious' (18.8 days) than on MM.111 (22.3 days for both). However, rootstocks generally had little effect on time to 50% flowering in the trees with the four different growth habits.

Scion differences were evident in the quantity of flowers produced but there were few rootstock effects. The spreading-round growth habit had three-times and SW had nearly two-times more flowers than UN growth habits (0.22, 0.12, and 0.07 flower clusters/cm^2 limb area, respectively). Lower bud production was observed previously in UN than in the spreading growth habits (Zagaja and Faust, 1983), and fewer flowers were expected. In 2003, rootstock affected flower and yield efficiency only in UN, which produced few flowers and only 3 fruit per tree on seedling rootstock. Nearly 63 fruit per tree were harvested from UN grown on M.9. More differences in yield due to rootstock were found in 2004 (Table 2).

3.3. Shoot growth components

Scion differences occurred with SW, SR, 'Golden Delicious', and 'Delicious' having longer average internode length than UN and UR (Table 3). Rootstock effects were not consistent among growth habits. For example, M.9 reduced average internode length in UR and UN growth habits but did not affect SW growth habit and actually increased internode length in the SR growth habit. In 2002 growth, M.9 reduced average internode length compared with seedling rootstock in UN and SW but not in UR and SR growth habits (data not shown). In 2002, internode number was not reduced by any rootstock except by M.7 with 'Delicious' (data not shown). No rootstock consistently reduced length or number of internodes in a 1-year-old shoot reflecting the variability in 1-year shoot growth among the different scion–rootstock combinations and even within the canopies of individual trees.

More branches grew in the trees with upright growth habits than spreading growth habits and most of these branches were less than 3 cm long (Table 4). Rootstock did not affect shoot growth as a main effect but rootstock–scion interactions occurred. M.9 rootstock had fewer branches, less branch growth, and less distance from the shoot terminus to the first lateral branch than other rootstocks in UN but M.9 had no effect on number of branches in UR or in SW growth habits.

Table 4
Branching characteristics of 1-year-old shoots of four apple growth habits on four rootstock and two apple cultivars on three rootstocks

Scion	Rootstock	Branches < 3 cm long		Branches > 3 cm long		Terminus to first branch	
		Number	Length (cm)	Number	Length (cm)	Internode (no.)	Length (cm)
Upright-round	M.9	5.3 a	3.3 a	1.5 a	11.5 a	20.8 a	5.9 a
	M.7	7.3 a	3.3 a	0.3 a	0.9 a	16.3 a	11.1 a
	MM.111	7.1 a	4.0 a	0.3 a	1.6 a	20.9 a	10.8 a
	Seedling	3.5 a	2.1 a	0.6 a	3.6 a	20.7 a	10.0 a
Upright-narrow	M.9	2.8 c	2.7 c	0.3 c	4.8 d	21.4 b	9.8 c
	M.7	6.0 bc	4.3 bc	0.9 bc	19.8 c	35.7 a	19.2 b
	MM.111	6.6 b	5.7 b	1.2 b	29.6 b	31.9 a	22.9 ab
	Seedling	9.4 a	7.4 a	1.7 a	36.7 a	36.4 a	25.1 a
Spreading-round	M.9	0.0 a	0.0 a	0.3 a	9.1 a	7.1 a	14.3 a
	M.7	0.0 a	0.0 a	0.1 b	4.8 b	3.6 ab	4.3 b
	MM.111	0.0 a	0.0 a	0.1 b	3.4 b	2.7 ab	4.8 b
	Seedling	0.0 a	0.0 a	0.0 b	0.0 b	0.0 b	0.0 b
Spreading-weep	M.9	0.4 a	0.6 a	0.1 a	4.3 a	8.3 a	13.0 a
	M.7	0.3 a	0.4 a	0.1 a	0.4 b	4.0 ab	5.7 ab
	MM.111	0.1 a	0.3 a	0.0 a	0.0 b	3.4 ab	7.2 ab
	Seedling	0.0 a	0.1 a	0.0 a	0.9 b	1.9 b	3.5 b
'Delicious'	M.7	0.1 b	0.1 b	0.1 a	1.4 a	5.3 a	5.5 a
	MM.111	0.4 a	0.5 a	0.0 b	0.0 b	4.8 a	5.3 a
	Seedling	0.1 b	0.1 b	0.0 b	0.0 b	1.5 a	3.1 a
'Golden Delicious'	M.7	0.0 a	0.0 a	0.1 b	1.3 b	2.6 b	4.0 b
	MM.111	0.0 a	0.0 a	0.2 a	7.4 a	7.2 a	9.6 a
	Seedling	0.0 a	0.0 a	0.0 b	0.0 b	0.2 b	0.4 b
$P > F$							
Scion (S)		0.01	0.01	0.01	0.01	0.01	0.01
Rootstock (R)		0.11	0.01	0.46	0.72	0.41	0.41
S × R		0.01	0.01	0.01	0.01	0.01	0.01

Within each growth habit and variable (column), means followed by the same letter do not differ at the 95% level of confidence.

4. Discussion

In this experiment, growth rate of trees with spreading growth habits was much greater early in the growing season than trees with upright growth habits. Trees with spreading growth habits tended to be taller, wider, have larger trunk diameters, and longer internodes. Rootstock proportionately affected both number and length of internodes within each growth habit so that average internode length was not significantly affected (Table 3). Trees on their own roots from the F2 generation of hybrid seedlings that were the source of scions used in the current experiment were studied previously. As in the current experiment, spreading growth habits tended to have longer internodes with larger, more vigorous trees than upright ones (Faust and Steffens, 1993; Jaumein and Faust, 1984; Zagaja and Faust, 1983). However, continuous variation of internode lengths were found within a tree size class, indicating that short internodes can occur in large trees and that separate genetic mechanisms regulated tree size and internode length (Zagaja and Faust, 1983). We also found variation of internode lengths, but the average internode length per annual shoot and tree size was consistent for a growth habit, indicating that the separate mechanisms that regulate internode length and tree vigor as reported by Zagaja and Faust (1983) may be genetically linked.

Duration of shoot elongation has also been related to internode length. 'Golden Delicious' trees with long internodes stopped shoot elongation by the end of June and growth habits with short internodes continued to elongate throughout the season (Grochowska and Buta, 1984; Faust and Steffens, 1993). In the current study, shoot elongation rates differed markedly with the long internode scions slowing growth by June, but elongation continued at a reduced rate to the end of the growing season. More fruit grew on trees with spreading than upright growth habits and reduced growth may have been, in part, due to fruit load (Fig. 3; Table 2). It is also possible that the season-long growth was a general rootstock effect since Faust and Steffens (1993) worked with own rooted trees. However, in the current study, differences in growth duration due to rootstock were not found.

Stem length can be shorter in scion on dwarfing rootstock due to slower elongation and early termination of seasonal growth to reduce the number of internodes (Webster and Wertheim, 2003). Growth of ungrafted M.9 rootstock was low and slowed near zero between 18 July and 12 August, in contrast to MM.111 which grew more quickly and did not slow appreciably during this time (Kamboj et al., 1997). In the current experiment during April, M.9 rootstock reduced growth more in the upright than the spreading growth habits but after April M.9 growth rates were similar for all growth habits

(Fig. 3). Although the quantitative effects of the size-controlling rootstocks differed with scion, the pattern of seasonal growth and branching remained consistent for each growth habit, regardless of rootstock. These rootstock–scion effects could significantly affect grower management practices, such as summer pruning and plant growth regulator application to control vegetative growth. Apple tree growth habits with rapid early-season elongation such as the SW and SR may require intensive management earlier than growth habits with slower early-season growth such as UR and UN. Requirements for cultural management of these growth habits may also be rootstock-specific; e.g. rates of a tree growth regulator could be adjusted differently for SW and SR on either MM.111 or M.9 due to differential growth control of the rootstocks on the scions.

Branch angle measurements confirmed visual impressions that UR was most upright, UN and 'Delicious' were next most upright, and 'Golden Delicious', SW, and SR had the widest branch angles and the most spreading canopies (Table 3). Previous research indicated that crotch angles of scion were narrower when budded on dwarf than on more vigorous rootstock (Warner, 1991). This rootstock effect on crotch angle was only observed on scions with upright growth habit and not on scions with a spreading growth habit. In our experiment, 'Golden Delicious' branches were more upright on M.7 than MM.111 or seedling rootstock. In general, branch angle differed by scion but was not affected by rootstock (Table 3).

Rootstock effects on whole tree dimensions were in accord with expectations. Generally, the largest-to-smallest trees grew on seedling, MM.111, M.7, and M.9 rootstocks. These rootstocks did not maintain tree size or shoot elongation by the same amount in all growth habits. Differences in the relative ranking of size-controlling rootstocks on tree size are unusual but can occur (Ferree et al., 1995). Although M.9 tended to reduce growth most, the percent growth reduction differed even between scions with similar growth habits. For example, M.9 reduced tree heights of SW and SR growth habits by 36 and 13%, respectively. The prevalence of rootstock-growth habit interactions highlights the complexity of root–shoot communication in grafted fruit trees. In the current experiment, scion appeared to have the dominant influence on tree architecture and rootstock modified growth rates. In previous work with trees that were siblings of the scions used in the current experiment, size-controlling effects were not associated with root-produced signals. Scions of less vigorous F2 seedlings budded to seedling rootstock remained dwarfed, suggesting that the dwarfing feature was not associated with a factor translocated from the root of the dwarf seedling (Steffens and Hedden, 1992). In addition, scions of standard trees grafted on to roots of less vigorous seedlings from the F2 generation were not dwarfed, reinforcing this finding. The current research agrees with Steffens and Hedden (1992) in that rootstock did not strongly modify the scion architecture (growth habit and branching characteristics).

In a study with F2 generation hybrid seedlings that were related to the trees used in the current experiment, less vigorous trees had greater phloem to xylem ratios and shorter internodes than the more vigorous trees (Jaumein and Faust, 1984). The altered anatomy of these dwarf seedlings may have been caused by high auxin levels in the phloem and a hormone imbalance (Grochowska and Buta, 1984). The UN trees in the current experiment were similar to the medium vigor trees used by Jaumein and Faust (1984). It is possible that hormone and anatomical characteristics of both scion and rootstock may account for differences in size-controlling effects observed in the current experiment.

The bud break pattern and branch orientation in UN trees suggested a hormone-mediated effect. The upright, antigravitrophic growth may be an auxin-related response associated with high auxin concentrations in UN shoots. Grochowska and Buta (1984) found high auxin levels in low vigor trees with short internodes (e.g. UN trees in our experiment). In the current experiment, multiple buds broke but most of the distal buds did not elongate on 1-year-old shoots and the distance from the terminal bud to the first branch was greatest in UN growth habits (Table 4). The phenomena of apical control (regulation of branch elongation; Zimmermann and Brown, 1971), rather than apical dominance (regulation of bud break), may effect the UN growth habit but the role of hormones in this canopy development is open to speculation. In the future, improved knowledge of the processes responsible for such scion–rootstock interactions can advance efforts to select or manage for needed apple tree growth habits (Kelsey and Brown, 1992).

Branching has been affected by rootstock. Schechter et al. (1991) found that rootstock did not affect dates of scion ('Starkspur Supreme Delicious') bud break, full bloom, and establishment of full canopy but differentially affected the number of spurs per cm limb circumference. In our experiment, rootstock did affect branch development with M.9 decreasing the number of <3 cm and >3 cm branches in UN compared with seedling rootstock.

5. Conclusion

This research reports the nature of size-controlling rootstock effects on apple scions with diverse growth forms. Overall tree size, internode length, shoot elongation rate, time to budbreak, and branch angle, were most influenced by scion. The hypothesized effects of rootstock decreasing branch angle or reducing growth most in upright growth habits were not supported. Rootstock size-controlling effects were as expected and the most-to-least dwarfing rootstocks were M.9, M.7, MM.111, and seedling. Shoot elongation rates were modified by rootstock but these effects were somewhat inconsistent. Bud break and monthly elongation rates of similar growth habits were not similarly affected by the same rootstock. These scion–rootstock interactions may be exploited to obtain trees with particular architectures such as reduced branching but wide-angled trees.

This research demonstrates that rootstock controls the size but does not markedly alter growth habit of apple shoots. The experiment was designed to investigate fundamental relationships of rootstock and scion without confounding effects of management practices. Further research would be necessary to determine the effects of pruning and training on rootstocks and scions with different growth habits. We conclude that apple tree

architecture (e.g. upright versus spreading and branching patterns) is not fundamentally modified by rootstock and that desired canopy architecture can be obtained in apple by management practices and breeding.

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